

THE LIFE CYCLE OF *CORYMORPHA* (= *EUPHYSORA*) *BIGELOWI*
(MAAS, 1905) AND ITS SIGNIFICANCE IN THE SYSTEMATICS
OF CORYMORPHID HYDROMEDUSAE

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The systematic interrelationships of medusae and polyps in the hydrozoan family Corymorphidae are, as yet, unclear in their details. The metagenic nature of the life cycle of *Corymorpha nutans* Sars was among the first such cycles described (Sars, 1835), but progress toward a unified systematics of the family has been slow. In its original usage, the polyp genus *Corymorpha* included a heterogeneous mixture of several separate evolutionary lines. Kramp (1949) proposed that polyps previously collected under this name were of at least two lineages, one associated with the medusa genus *Euphysa* Forbes (1848) and the other associated with the medusa genus *Steenstrupia* Forbes (1846). He resurrected the polyp genus *Heteractis* (Allman, 1872) for polyps which differ from typical *Corymorpha* by their permanently capitate oral tentacles, their strongly contractile moniliform aboral tentacles, their lack of a parenchymous diaphragm separating the hypostome from the hydrocaulus, their replacement of a basal tuft of root-filaments by a belt of papillae in the upper hydrocaulus, and by differences in perisarc structure (Kramp, 1949, p. 185). A compelling argument for the subdivision of the family was the observation that the medusae produced by *Heteractis* polyps were invariably species of *Euphysa* and that the only medusa known from typical *Corymorpha* polyps was a *Steenstrupia*. However, since all *Euphysa* medusae had not been linked to *Heteractis* polyps and all metagenic *Corymorpha* polyps had not been associated directly with *Steenstrupia* medusae, Kramp retained a dual classification system under which the specific name was shared by both life cycle stages, but the polyp and medusae retained their "classical" generic designations. This taxonomic device was accepted by some systematists (e.g., Russell, 1953), but has been disputed by others (Rees, 1957; Naumov, 1960; Brinckmann-Voss, 1970). Despite differences of opinion on matters of nomenclature, the separation of the family Corymorphidae into distinct lines is generally accepted. Indeed, Rees (1957) recognized four sub-families (Euphysinae, Corymorphinae, Boreohydrinae, and Branchiocerianthinae), thereby re-establishing the Euphysinae of Haeckel (1879) to emphasize the distinctiveness of the *Euphysa* (= *Heteractis*) line.

Within this systematic framework, the position of the genus *Euphysora* has

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remained totally obscure. Since its erection by Maas in 1905, this medusa genus has had a complex taxonomic history. It has at various times been combined with either *Euphysa*, *Corymorpha* (as *Steenstrupia*), or both. Hartlaub (1907) immediately reassigned the type species, *Euphysora bigelowi* Maas, to the genus *Corymorpha* within the subgenus *Euphysa*; and Mayer (1910) combined *Euphysora* and *Euphysa* into *Corymorpha*. Vanhöffen (1911) and Browne (1916) thereupon retained *Euphysora*, but little more than a decade later Uchida (1927) assigned *E. bigelowi* to *Euphysa*. The following year Kramp (1928) argued for the retention of *Euphysora*, further suggesting that the genus was more closely allied to *Corymorpha* than to *Euphysa*. While demonstrating the distinctness of the polyp stages of *Euphysa* and *Corymorpha*, Kramp (1949) did not speculate further on the position of *Euphysora*.

The ambiguity in the systematic position of *Euphysora* arose for three reasons. First, the criteria upon which Maas (1905) based this new genus were felt by some workers to be arbitrary and susceptible to individual interpretation (Mayer, 1910). Secondly, the genus as currently constituted (Kramp, 1961) may be a heterogeneous mixture of species (Kramp, 1948). Finally, and most significantly, the polyp stage has not been described for any species of *Euphysora* (Kramp, 1961).

In this paper the life cycle of the type species, *Euphysora bigelowi*, is described. On the basis of this life cycle it is necessary to revise the nomenclature of *Euphysora* to reflect a close alliance with the higher Corymorphines and to continue the recent trend of elimination of dual classification in hydrozoans (Rees, 1957; Naumov, 1960; Brinckmann-Voss, 1970). The implications of this revision on the systematic positions of other members of the medusa genus are also discussed.

MATERIALS AND METHODS

Five sexually mature corymorphid medusae, later identified as *Euphysora bigelowi*, were collected in a plankton tow in Monterey Bay, on September 24, 1973. The net (0.5 m diameter) was towed on a weighted 15 m line at very slow speed for about 30 min, and was on the bottom during part of the tow (some sediment was recovered with the sample).

The medusae were returned to the laboratory, fed brine shrimp nauplii, and left in a small finger bowl at about 14° C for several days. They died shortly thereafter and disintegrated. At this time, however, metamorphosing larvae were noticed on the bottom of the bowl and the sea water was replaced. Within a week these larvae had completed metamorphosis into eight polyps. Several polyps were transferred to the Bodega Marine Laboratory for culture; the remainder were maintained at Stanford.

The first evidence of gonosome development in the Stanford culture was on October 17, 1973, and the first medusa was liberated on December 5, 1973. The Stanford culture deteriorated shortly thereafter, and the line was lost in January, 1974. Attempts to rear young medusae on brine shrimp nauplii were unsuccessful. The descriptions which follow are based on a preserved polyp, five newly released medusae preserved within 24 hr of liberation, notes made on living polyps and

medusae, and extensive photographic records of various stages. The polyp and five newly released medusae have been deposited at the National Museum of Natural History (#56762 and #56760).

RESULTS

Adult medusa

An adult medusa is shown in Figure 1c. The medusae were corymorphid in morphology with three short simple tentacles and one long tentacle which differed from the others in form as well as size. All tentacles were hollow. The length of the bell ranged up to 5.0 mm. When extended, the manubrium reached the umbrellar margin and sometimes protruded slightly beyond. The edges of the mouth were armed with nematocysts. The apical projection was produced as a conical process with an apical canal extending about two thirds of the way to the tip. The primary tentacle was as long as the bell and was studded with as many as eight (possibly nine) subterminal nematocyst bulbs along its length. The largest specimen had a large, club-shaped terminal bulb which may have represented a small terminal bulb and a ninth subterminal bulb in the process of division. All subterminal nematocyst bulbs were adaxial in orientation. The remaining three tentacles were short and simple, and were not armed with nematocyst bulbs, but with scattered nematocysts. The two tentacles adjacent to the primary tentacle, the "lateral" tentacles (Kramp, 1928), were twice as long as the one opposite. The morphology of these medusae was well within the range of variation of previous descriptions of *Euphysora bigelowi* (Maas, 1905; Browne, 1916; Uchida, 1927; Kramp, 1928).

Zoogeographic records of *Euphysora bigelowi* indicate a wide, warm-water distribution. Since its original collection in the Malay Archipelago (Maas, 1905), its known distribution has been extended to include the Indian Ocean (Browne, 1916), northeastern Australia (Kramp, 1953), and southeastern Japan (Uchida, 1938; Yamazi, 1958). It ranges westward across the Pacific Ocean to the Palau Islands (Uchida, 1947) and has been reported from Chile (Kramp, 1952). Kramp (1968) later suggested that the Chilean record might be erroneous, although it now appears less suspect. The collection of *Euphysora bigelowi* in Monterey Bay, California, is rather surprising and is inconsistent with all previous records except that of Chile. The Monterey Bay collection represents a substantial range extension (of about 8,000 km) into the northeastern Pacific Ocean.

In comparing the various descriptions of *Euphysora bigelowi* with the California material, it is clear that there is extensive morphological variation in this species, both within and between populations. Characters which have proven to be quite variable are the presence or absence of the apical canal, the relative lengths of the three secondary tentacles, and the relationship between bell height and the number of nematocyst bulbs on the principle tentacle. Populations from the Malay Archipelago (Maas, 1905) included animals with and without apical canals; and Kramp (1928) reported variation for specimens from the Sunda Strait (the predominant type there was lacking the canal). Other descriptions

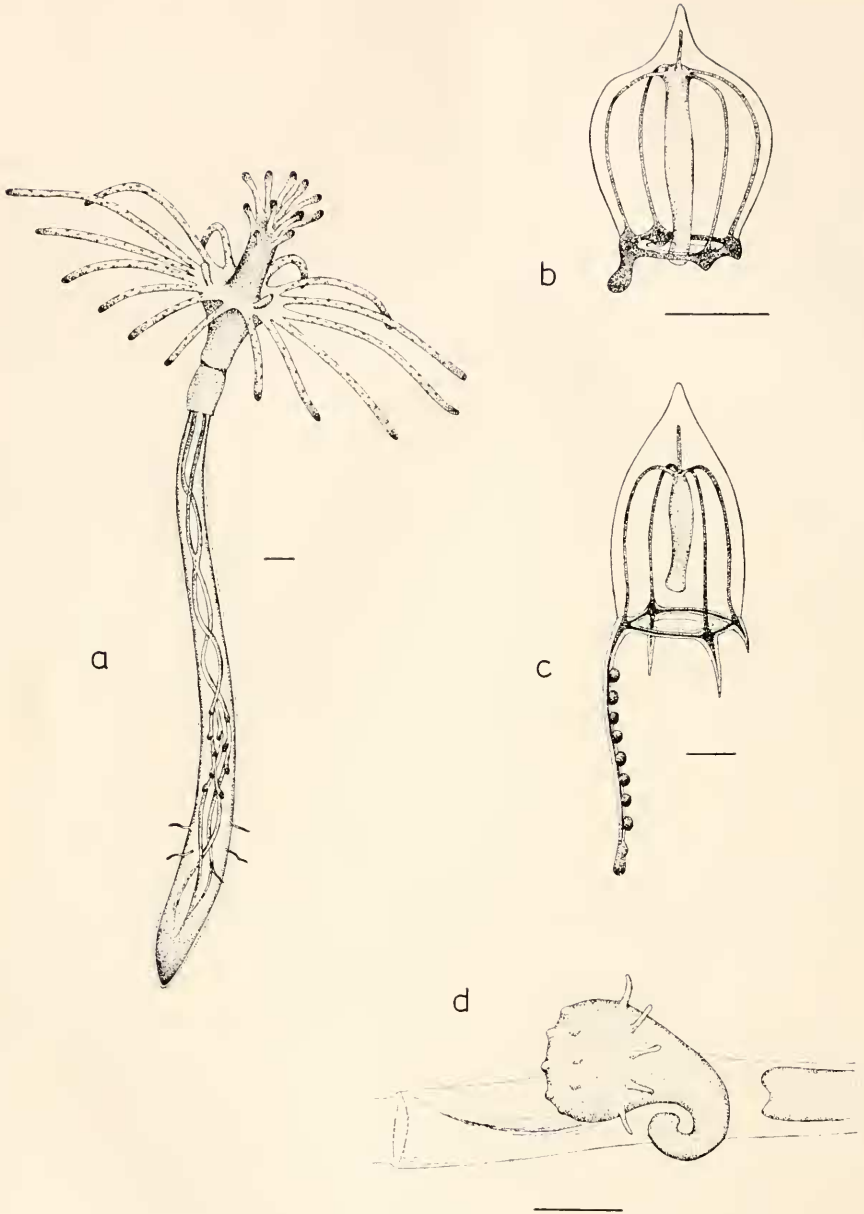


FIGURE 1. Stages in the life cycle of *Corymorpha* (= *Euphysora*) *bigelowi*: a, composite drawing of the mature polyp illustrating its general aspect and emphasizing characteristic features; b, the newly released medusa; c, the adult medusa; d, polyp reproduction by frustulation (the fragmented base of the parental polyp is shown to the right of the metamorphosing bud). Scale bar is 1.0 mm for (a) and (c) and is 0.5 mm for (b) and (d).

(*e.g.*, Browne, 1916; Uchida, 1927) indicate the complete absence of apical canals in animals from the Indian Ocean and off Japan. The California specimens, in contrast, all had well-developed apical canals. Variation in the relative lengths of the three secondary tentacles is also substantial. Kramp (1928) tabulated the relative lengths of the "lateral" and "opposite" secondary tentacles for the Sunda Strait specimens. His analysis indicated that the opposite tentacle is shorter than the other two in small specimens (1.5 mm high), but that its relative length increases with medusa size and may eventually exceed the lateral tentacles in length (in 2.25 to 3 mm high medusae). In contrast, Browne (1916) noted that in his small specimens the three secondary tentacles were of equivalent length, but that in the larger specimen (4 mm high) the opposite tentacle was much shorter than the lateral tentacles. In the California specimens the opposite tentacle was substantially shorter than the other two, even in the largest (5 mm high) medusa (Fig. 1c). There appears to be differential development of the secondary tentacles, with variation among populations. For this character our specimens are more like those from the Indian Ocean than those from the Sunda Strait. A third morphological feature showing substantial variation is the number of nematocyst bulbs on the principal tentacle. This character seems to be related to medusa height (Browne, 1916; Kramp, 1928), but the degree to which the number of bulbs increases per unit change in medusa height seems to vary among populations. For example, a 4.0 mm high medusa from the Indian Ocean had 11 nematocyst bulbs (Browne, 1916), whereas a 2.25 mm medusa from the Sunda Strait had 21 bulbs, and one individual 1.5 mm high had 31 (Kramp, 1928). Uchida (1927) illustrates a 3.5 mm medusa with 26 subterminal bulbs. For this character the California sample is more similar to that from the Indian Ocean than to the Sunda Strait or Japanese collections. Variation in the three characters does not appear to be correlated. The California specimens resemble those from the Indian Ocean with regard to the lengths of the secondary tentacles and the number of nematocyst clusters on the primary tentacle, but in one group the apical canal was uniformly lacking and in the other it was uniformly well-developed. The use of these characters in delineating the genetic relationships between populations in different parts of the species range will probably not be very productive.

Morphology of the polyp

The following description was made from a polyp grown in the laboratory until preservation on December 12, 1973, and from notes and photographs of live polyps in culture. The preserved specimen is 13 mm high and about 1 mm wide at its widest point. The hypostome is 3 mm high and also about 1 mm wide. There is considerable variation in dimensions depending upon the state of expansion in live individuals. Figure 1a illustrates the general aspect of the polyp and emphasizes some of the characteristic morphological features. Figure 2a shows the hypostome and the early gonosome of a mature polyp.

Among individuals there are between 15 and 20 aboral filiform tentacles (beset with scattered nematocysts) in a single whorl. These tentacles are apparently not very contractile; our photographs do not include any in which the aboral

tentacles are substantially contracted despite the use of intense lighting and the occasional addition of brine shrimp nauplii during photographing. In mature polyps there are up to 35 oral tentacles (with scattered nematocyst batteries) set in irregular rows on the hypostome. Although the oral tentacles are not distinctly capitate, they may be somewhat thickened at their tips, particularly in young polyps. A diaphragm separates the hypostome from the polyp body (Fig. 1a). The hydrocaulus is enclosed in a thin, membranous perisarc which is attached to an annular ring of thickened ectoderm slightly below the diaphragm. In some specimens the perisarc extended beyond the base of the hydranth in the form of a thin tube. The body is slightly inflated at its base to a width of about 1.5 mm. Anchoring rootlets with inflated tips and varying in width between 25 and 50 μm arise from prominent endodermal canals which are visible in the hydrocaulus (Fig. 1a). The medusa buds are mounted in clusters on inflated pedicels which arise from the hypostome between the oral and aboral tentacles, but much nearer the aboral tentacles (Fig. 2a). These pedicels are not very long (1 to 2 mm) and are not highly branched (Fig. 2b).

Gonosome development and the newly liberated medusa

Gonosome development was first observed about two weeks after larval metamorphosis. Subsequent development of the medusa buds was substantially slower than initiation of the gonosome, and the first medusa was not released until about six weeks after the gonodendra were first visible.

The gonodendra develop asynchronously on the polyp, several stages of progression being found on the same hydranth. The earliest structure is a simple tubular projection from the hypostome immediately above the aboral tentacles. This projection elongates and branches, the medusa buds forming at the termini of each branch (Fig. 2b). The differential development of the primary tentacle of the medusa takes place during attachment to the gonodendra and the manubrium swells to occupy most of the subumbrellar cavity (Fig. 2c). Approximately a day before liberation the attached medusa falls below the whorl of aboral tentacles (Fig. 2d) by which time the medusa is contractile, but is not rhythmically pulsating. It is released (or breaks free) with an incompletely formed apical chamber at a size of about 1.3 mm high by 1.2 mm wide.

The newly released medusa (Fig. 1b) is colorless except for pale yellow tentacle bulbs. The manubrium is tubular and extends to the velar opening or slightly beyond. The apical canal is variable in development, extending from one-sixth to two-thirds of the way to the tip of the apical projection. This range of variation is found even between individual medusae released from the same polyp. The tip of the apical projection has small papillae on its surface. Only one tentacle is developed to any appreciable degree, the others being reduced to conical projections. The primary tentacle bears a club-shaped terminal nematocyst bulb, but is lacking the subterminal adaxial bulbs of older medusae. Nematocysts are present on all tentacles, but are lacking on the exumbrellar surface.

The asynchronous development of the gonosome results in a prolonged period of medusa liberation. One polyp was censused daily and produced a total of 34 medusae over a period of three weeks. Newly released medusae were not

seen to feed on brine shrimp nauplii and did not live for more than a few days.

The newly released medusae are similar in size to the smaller individuals described from plankton collections by Kramp (1928) and Browne (1916). It is of interest to note that in these collections small individuals (1.25 to 1.5 mm high) have subterminal nematocyst bulbs on the primary tentacle which are absent on the newly released *Euphysora bigelowi* medusae. In *Corymorpha nutans* the annular subterminal bulbs are developed even before liberation from the polyp (Russell, 1953).

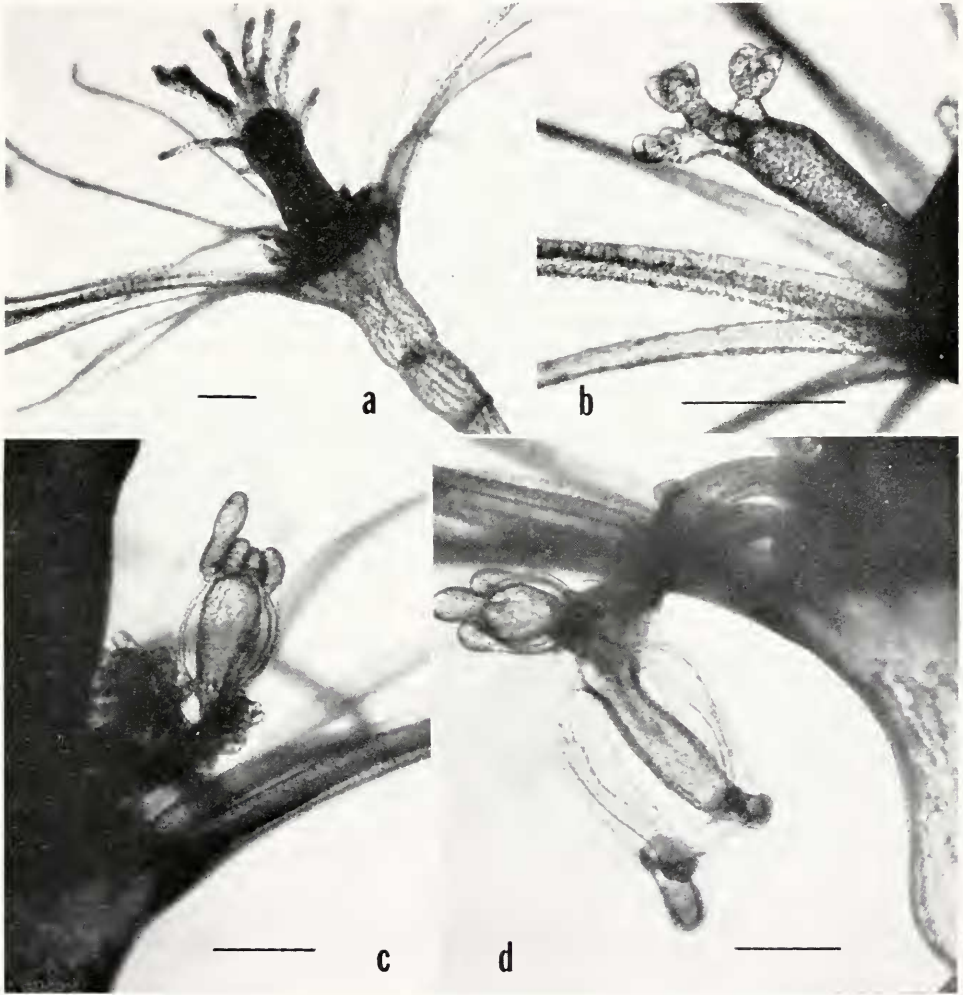


FIGURE 2. The development of the gonosome of *Corymorpha* (= *Euphysora*) *bigelowi*: a, lateral view of the hypostome of a polyp with early gonodendra; b, immature gonophore with inflated pedicel and developing medusa buds; c, medusa buds in advanced state of development (note the enlarged manubrium and primary tentacle); d, medusa just prior to release. Scale bar is 0.5 mm.

TABLE I

Cnidom of Corymorpha (= Euphysora) bigelowi, with measurements in microns.

Stage	Stenoteles (large)	Stenoteles (small)	Microbasic mastigophores	Desmonemes	Anisorhizas*
Polyp					
Oral and aboral tentacles	13-16 × 8.5-10	7-8 × 4.5-5	7.5-8.5 × 3-4	4-6 × 3.5-4.5	
Newly released medusa					
Tentacles	11-15 × 9-12	8-10 × 7-8	4.5 × 9.5	6.5-9 × 3.5-5.5	
Adult medusa**					
Primary tentacle	13-14 × 11-12	7.5 × 7		5 × 10	
Secondary tentacle	11 × 13	8-9 × 7			11 × 12
Lips of mouth	12-14 × 10-12	6 × 7			
Umbrella		7 × 9	3 × 8		9 × 10

* No fired nematocysts of this type were closely examined.

** Measurements from photographs of tissue squashes.

Cnidom

Data on the sizes, types, and locations of nematocysts present in different stages of the life cycle are given in Table I, and selected types are illustrated in Figure 3. Four types of nematocysts were found: stenoteles, microbasic mastigophores, desmonemes, and probably anisorhizas. These four types have been previously reported in two related species, *Corymorpha nutans* Sars and *Ectopleura dumortieri* (Van Beneden) (Russell, 1938; Weill, 1934). In *Euphysa aurata* Forbes the heteronemes and desmonemes have not been found and atrichous haplonemes are present (Rees, 1957).

Mode of polyp asexual reproduction

Asexual polyp reproduction was observed once. The terminal portion of the base of the polyp detached from the remainder of the hydrocaulus, and within a few days this fragment began development of both oral and aboral tentacles and broke free of the parental perisarc (Fig. 1d). This mode of reproduction has been termed "frustulation" by Kramp (1948) to emphasize its relationship to transverse fission and its distinctness from true budding. It is apparently a normal process of reproduction in several species of *Euphysa* (e.g., Miles, 1937) but has not been reported for *Corymorpha* (Kramp, 1949) in which other forms of asexual reproduction, such as polyp development from root filaments, are observed (Ikeda, 1910; Kramp, 1949).

DISCUSSION

The polyp reared from *Euphysora bigelowi* demonstrates the following structural features which are characteristic of the genus *Corymorpha*: an irregularly

arranged cluster of oral tentacles, a single whorl of aboral tentacles with scattered (as opposed to annular) nematocyst batteries, an annular diaphragm, rooting filaments borne only in the lowermost part of the hydrocaulus, gonophores borne in clusters on pedicels (gonodendra), and well developed endodermal canals in the lower part of the hydrocaulus. Indeed, the parenchymous diaphragm and endodermal canals are considered to be characteristic of advanced and highly specialized members of the genus (Kramp, 1949). However, the polyp of *E. bigelowi* also shares certain features with *Euphysa*-type polyps. The initially somewhat capitate oral tentacles of *E. bigelowi* apparently do not become completely filiform in older polyps and are intermediate between *Corymorpha* and *Euphysa* in this regard. The curious mode of asexual reproduction by frustulation (Fig. 1d) has been reported in *Euphysa* (Miles, 1937) but not in *Corymorpha* (Kramp, 1949). The perisarc of *E. bigelowi* is reminiscent of *Euphysa* both in its attachment to the upper region of the hydrocaulus and in its extension beyond the base of the hydrocaulus. We do not know the extent to which peculiar environmental factors of our culture conditions may have influenced the expression of these characteristics, or the degree of phenotypic plasticity in this species. Modes of budding in hydro-

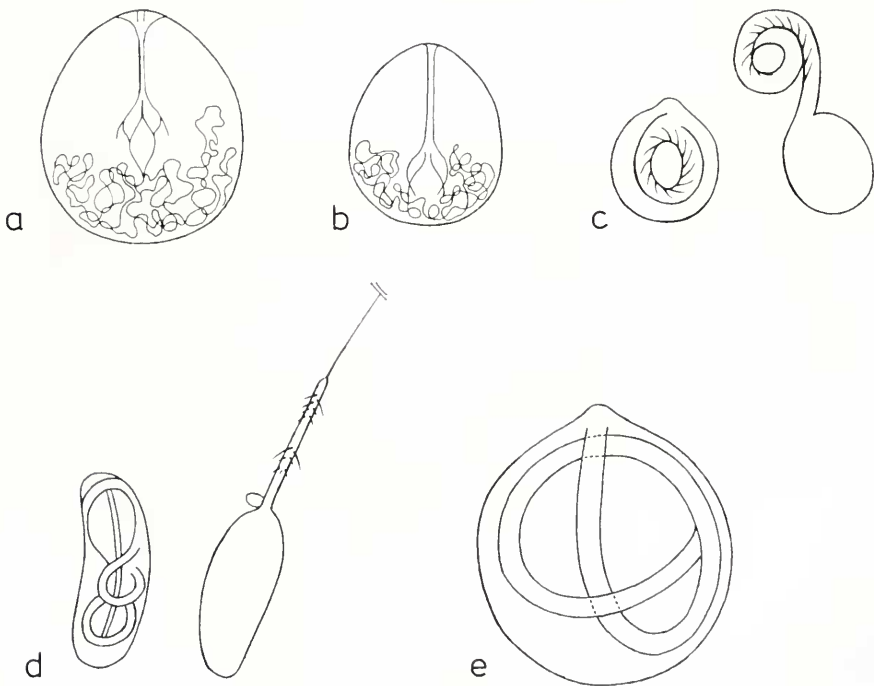


FIGURE 3. The cnidom of *Corymorpha* (= *Euphysora*) *bigelowi*: from aboral tentacle of polyp (a-c)—a, large stenotele, b, small stenotele, c, undischarged and discharged desmoneme; d, undischarged and discharged microbasic mastigophore from oral tentacle of polyp; e, anisorhiza (?) from secondary tentacle of adult medusa. Scale bar is 10 μ .

zoans are quite variable, and bizarre forms can be produced under unnatural culture conditions (Sassaman, 1974).

The substantial similarities of the reared polyp to *Corymorpha* far outweigh in significance the minor deviations from the typical form; thus, the polyp can be relegated to the genus *Corymorpha*. *Corymorpha nutans* is the only other metagenic polyp in the genus whose medusa is known. Following recent efforts in eliminating the dual classification system which has bedeviled hydrozoan systematics from its inception (Rees, 1957; Naumov, 1960; Brinckmann-Voss, 1970), it is deemed appropriate to refer to both the polyp and the *Euphysora bigelowi* medusa as *Corymorpha bigelowi*, since *Corymorpha* (Sars, 1835) precedes *Euphysora* (Maas, 1905).

Since this revision is based on the type species of the genus *Euphysora*, and the genus is believed to be a heterogeneous mixture of species (Kramp, 1948), other medusae previously assigned to *Euphysora* are of an uncertain status. These species are *E. gracilis* (Brooks, 1882), *E. annulata* (Kramp, 1928), *E. furcata* (Kramp, 1948), *E. gigantea* (Kramp, 1957), *E. normani* (Browne, 1916), and *E. valdiviae* (Vanhöffen, 1911). This assemblage includes species which resemble *C. bigelowi* in having unbranched primary tentacles (*E. annulata* and *E. gracilis*), species with branched primary tentacles which lack subterminal nematocyst bulbs (*E. furcata*, *E. gigantea*, and *E. valdiviae*), and two species (*E. valdiviae* and *E. normani*) with exumbrellar nematocyst tracts. This latter condition may be a more primitive condition than is typical in *Corymorpha* (Rees, 1957). Ultimate resolution of the systematic positions of these various species will require additional life cycle data.

It is uncertain whether or not the polyp of *C. bigelowi* has been found in nature. No polyps similar to *C. bigelowi* are known from central California. Extensive hydroid collections by the Allan Hancock Foundation Expeditions (Fraser, 1948) have not yielded any local metagenic *Corymorpha*, and the Pacific fauna, in general, includes few metagenic *Corymorpha* species. Uchida (1927) suggested either *C. tomoensis* Ikeda or *C. carnea* (Clark) as the polyp stage of *Euphysora bigelowi*. The morphology of *C. tomoensis* (Ikeda, 1910) is similar to that of *C. bigelowi*, particularly the medusa buds. There are, however, substantial differences in hydranth size, number and morphology of the tentacles, complexity and development of the basal region, and mode of budding. In addition, *C. tomoensis* has not been reported from western North America (Fraser, 1948). *Corymorpha carnea* (Clark, 1876), while reported from North America, has not been adequately described, and its known distribution is restricted to northern Alaska (Torrey, 1902). At present, *C. bigelowi* cannot be positively associated with any other previously described species of *Corymorpha*, although *C. tomoensis* and *C. carnea* cannot be unequivocally eliminated. It is possible that the polyp phase of *C. bigelowi* has not yet been found in the field.

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SUMMARY

1. Five individuals of the corymorphid jellyfish, *Euphysora bigelowi* Maas, were collected in 1973 in Monterey Bay, California, for a range extension of more than 8,000 km across the northeastern Pacific Ocean.
2. Larvae released by these medusae were cultured and the resulting polyps, the first known from this medusa genus, are described.
3. The polyps are a *Corymorpha*, but share some minor characteristics with polyps of the corymorphid genus *Euphysa*.
4. The polyp and medusa are assigned the name *Corymorpha bigelowi* (Maas); the systematic implications of this revision are discussed.

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